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“..... per litora spargite muscum,
Naiades, et circum vitreos considite fontes :
Pollice virgineo teneros hic carpite flores :
Floribus et pictum, divæ, replete canistrum.
At vos, o Nymphæ Craterides, ite sub undas ;
Ite, recurvato variata corallia trunco
Vellite muscosis e rupibus, et mihi conchas
Ferte, Deæ pelagi, et pingui conchylia succo.”
Parthenii Ecl. 1.

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I.—*On the Anatomy of Eolis, a genus of Mollusks of the order Nudibranchiata.* By ALBANY HANCOCK and DENNIS EMBLETON, M.D., F.R.C.S.E., Lecturer on Anatomy and Physiology in the Newcastle-upon-Tyne School of Medicine.

[With five Plates.]

THE Nudibranchiate Mollusks are divided into two families, the *Doridae* and the *Tritoniadae*; the anatomy of the former was fully investigated by Cuvier, that of the latter, however, was only partially examined by that illustrious physiologist; and the *Eolidinae**, a very extensive division of it, were left totally unexplored, but were nevertheless considered to agree in organization with *Tritonia Hombergii*, the typical form of the group.

Recently however the attention of zoologists has been drawn to the subject by M. Milne Edwards, who was the first to point out that the *Eolidinae* deviate in a very striking manner from the rest of the family. He found in the genus *Calliopæa* a ramified digestive apparatus. This curious organ was supposed by that gentleman to perform the double function of digestion and circulation, and consequently to have analogy with the gastro-vascular system of the *Medusidae* on the one hand, and on the other with the *Nymphon*, on account of the cæcal prolongations of the digestive organ that penetrate the exterior branchial papillæ.

Since this discovery there has appeared in the ‘Annales des

* We use this name to designate the subfamily of which *Eolis* is the type.
Ann. & Mag. N. Hist. Vol. xv.

Sciences Naturelles' a very elaborate article by M. A. de Quatrefages on what that gentleman considers a new generic form, to which he has given the name *Eolidina paradoxum*; this he states differs from the typical organization, not only in its digestive apparatus, but also in many other respects, and in some instances in the most extraordinary manner.

The subject of M. de Quatrefages' memoir however does not vary in any external characters from *Eolis*, to some of the British species of which it is closely allied. We should therefore expect the anatomy of *Eolidina paradoxum* to coincide pretty accurately with that of *Eolis*, at least not to deviate from it to any extent in the more important organs; yet very considerable deviations do exist, if the observations of M. de Quatrefages be correct. Several of these observations however we are disposed to question.

Previously to the publication of the memoir just named, we had investigated the anatomy of *Eolis* in company with Mr. Joshua Alder, and although many of our results were borne out by those of the French naturalist, yet in several important particulars we found that we entirely disagreed with him. We have therefore reinvestigated the matter with much care, and particularly with reference to the points in dispute, and have been able to corroborate our original views in the most satisfactory manner.

The subject is of considerable interest, as it is principally on his views of the anatomy of *Eolidina* and two other allied species that M. de Quatrefages has proposed his order *Phlebenterata*.

It is therefore desirable that the anatomy and physiology of the *Eolidinæ* should be fully ascertained.

With a view to this we now publish the results of our researches, hoping that they may have the effect of fixing the attention of others more able than ourselves to inquire into the matter.

We would premise that, in the following paper, where no authority is given after the name of any species mentioned, it must be understood that that species has been described by Messrs. Joshua Alder and Albany Hancock.

We have chiefly turned our attention to *Eolis papillosa*, Johnston, probably *E. Cuvierii* of French authors, Pl. I. fig. 1; not more on account of its general resemblance in form to *Eolidina paradoxum* than for the advantages presented by its great size, which has enabled us to ascertain by actual dissection almost every point of importance.

Of this species we have had numerous specimens, both alive and in spirits, and in all stages of growth, from two lines to two inches in length.

It is slightly depressed, tapering more abruptly than usual to a point behind; both the dorsal and oral tentacles are simple, short and conical; the branchial papillæ are slightly compressed

and taper to a point; they are arranged down the sides of the back in about twenty transverse series of from twelve to eighteen papillæ each; the foot is broad, and slightly produced at the sides in front.

We have not however confined ourselves to this species, but have extended our inquiries to several others, for the purpose of showing how far the internal organization varies in the group.

E. olivacea, Pl. I. fig. 3, is thus frequently alluded to. It closely resembles the species described by M. de Quatrefages, and is in fact, according to the generic characters given by him, with the exception of a posterior dorsal anus, an *Eolidina*. It is generally about half an inch long, has four simple, slightly conical tentacles; the anterior part of the foot is rounded at the sides, or only slightly angulated; the branchial papillæ are cylindrical, and arranged down the sides in about seven transverse rows of four or five papillæ each.

E. coronata, Forbes, Pl. I. fig. 2, has also been examined with the same view. This species differs from the two former as much perhaps as any of the genus, and is therefore well calculated for our purpose. It is sometimes one inch and a half long, the body is almost cylindrical, and terminates in a fine point behind; the anterior lateral angles of the foot are somewhat produced; the oral tentacles are long and simple, the dorsal annularly laminated; the branchial papillæ are cylindrical, and arranged down the sides in six or seven clumps.

Besides these three, we have had upwards of twenty other species, to some of which we shall occasionally refer. A few of these have the anterior angles of the foot produced into tentacular points, as described by Cuvier; and others have the large vase-shaped branchial papillæ resembling those of the genus *Amphorina* of M. de Quatrefages.

During our investigations, we have used in the dissection of the organs the simple lens, and for the examination of the minuter parts of the organs, the tissues and fluids, one of Powell and Lealand's best compound microscopes. We have avoided using the compressor as much as possible, being aware that it is a great cause of error in studying the structure of animals so complicated and delicate as the *Eolidinæ*. These mollusks invariably contract themselves greatly when subjected to pressure, and the various organs are confusedly crushed together, so that it is quite impossible to distinguish any of them with precision. We have never succeeded in tracing in this manner the whole of any of the viscera, though we have several times made the attempt, and we can easily conceive that the compressor has led to many of the errors which we believe M. de Quatrefages has committed, though we give him full credit for the amount of information that he has

really gathered from the very limited number and minute size of his specimens.

We propose to treat of the anatomy of *Eolis* by describing successively the various organs, beginning with those of digestion, which will form the subject of the present article. The physiology will be found incorporated with the anatomy.

In Pl. V. fig. 16, is given a general view of the viscera of *E. papillosa*, the dorsal skin having been removed.

Organs of Digestion.

These consist of

- 1st. An outer and an inner lip, leading to
- 2ndly. A buccal mass, composed of a pair of horny plates, provided with strong cutting-edges, and inclosing a spiny prehensile tongue, having strong muscles adapted to produce all necessary movements. From the posterior part of the dorsal aspect of this mass passes backward,
- 3rdly. A short constricted œsophagus, which ends in
- 4thly. A ramified digestive cavity; the ramifications continued into the branchial papillæ, and developed into a more or less complicated follicular apparatus for the biliary secretion, being at the same time continued into ovate vesicles which open externally at the apices of the papillæ.
- 5thly. A short intestinal tube coming off from the posterior part of the dorsal aspect of the bulb of the stomach, and ending in an anus placed on the right side of the body.
- 6thly. Minute salivary glands.

The mouth, in *Eolis papillosa* (an anterior view of which, from a specimen that had been in spirit, is shown in Pl. V. fig. 14), opens on the inferior surface of the head and in front of the anterior border of the foot. It is provided with an external pair of large soft lips, Pl. I. fig. 4 *a*, that divide vertically on the median line. A little within these there is a strong, firm, somewhat compressed, muscular layer—the inner lip, Pl. I. figs. 4, 6, and 8 *b*, surrounding an oval vertical space, through which two strong, brown, hornylaminæ, the cutting-blades of the jaw, Pl. II. fig. 2 *a*, are visible. These blades are seen to be separated by a vertical fissure (Pl. V. fig. 14 *c*) opening into the cavity of the mouth. An inferior view of the mouth of *E. olivacea* in its natural state is seen in Pl. V. fig. 15.

The buccal mass itself, Pl. I. fig. 7, is composed of a pair of large corneous plates, a tongue, and the muscles necessary for the movements of these organs. It is a large and apparently compact body of a subtriangular form, with the sides a little compressed. The corneous plates, Pl. I. figs. 4 *a*, 9 *a a*, Pl. II. 5, 7, &c., are nearly co-extensive with the general mass, on the sides of

which they are placed, partially imbedded in the muscles. They are of an irregularly elliptical form, slightly concave internally and convex externally, and are gradually thinned to a fine edge at their inferior and posterior margins. From the superior margin of each plate near its anterior part projects inwards a triangular process, Pl. I. fig. 9 *b* and Pl. II. fig. 7 *a*; these processes are united at their apices on the median line by a strong ligament, forming a hinge-like joint or pivot on which the horny plates move easily. Below and a little in advance of these processes project downwards the two large arched cutting-blades, Pl. I. fig. 9 *c*, Pl. II. 5, and 7 *b*; these blades form the anterior edges of the corneous plates, and end inferiorly in long pointed processes, which are kept together by muscular insertions.

The upper surface of the processes for the hinge is divided unequally by a slight ridge, Pl. I. fig. 9 *a* and Pl. II. 7 *c*, into two parts; these give attachment to transverse muscles which move the horny plates upon the pivot: the muscle in front of the ridge, Pl. I. figs. 6 *c'*, 7 *d*, 10 *c*, and Pl. II. 2 *b*, is also in front of the pivot, and has the office of closing the jaws; that behind the ridge, Pl. I. figs. 6 *d*, 7 *e* and 10 *b*, is the opponent of the former and opens the jaws. The latter is much larger than the former and consequently stronger, and extends backwards as far as the œsophagus. There is however another transverse muscle, Pl. I. figs. 6 *e*, 10 *d* and Pl. II. 2 *c*, the duty of which is to assist in closing the cutting-blades. This muscle is seen attached to the edge of the horny plates at their anterior inferior aspect below the cutting-blades. The closure of the jaws is further materially promoted by a sphincter muscle which forms part of the lips, and will be described further on.

On the upper aspect of the buccal mass, behind, and partly covered by the transverse muscle that opens the jaws, and running on each side of the œsophagus backwards and then downwards, is a well-defined muscular layer, Pl. I. figs. 5 *a*, 7 *f* and 9 *e*, having its origin from the inner border of the horny plates. The fibres which arise the furthest forward form the inner edge of each muscle, and unite on the median line immediately behind the œsophagus; those which come off behind these pass parallel to them, and are united also on the median line at points successively further behind and below the former, and the fibres which are last in origin are prolonged and become lost upon the under aspect of the buccal mass. All the fibres of this muscular layer, besides uniting with each other, are attached by their anterior surface to the muscles of the tongue upon which they lie. One office of these muscles appears to be to pull forwards the œsophagus so as to close its orifice; their principal function we will explain when we come to the tongue.

On removing these muscles there is brought into view a very thin stratum of glistening muscular fibres, Pl. I. fig. 9 *f*, attached to the opposed edges of the horny plates and converging towards the œsophagus, upon which they pass, forming at once a coating of longitudinal fibres for that tube, and the attachment of it to the skeleton of the mouth. This delicate layer lies upon the lining membrane of the mouth and œsophagus.

On cutting through the hinge and separating the horny plates, we obtain a view of the interior of the mouth, Pl. I. fig. 8; here we find in the median line the arched prominent ridge of the tongue *c*, extending from before backwards, formed of seventeen or eighteen transversely curved imbricated plates, Pl. II. fig. 1, their posterior free edges thickened, of a dark chestnut colour, and presenting about forty spines slightly bent, and having their points directed backwards. This ridge is supported upon the curved apex of a wedge-shaped muscular mass, Pl. I. figs. 6 *f* and 8 *d*, that rises from the posterior inferior wall of the mouth, and is much thicker behind than before. A lateral view of this mass shows two sets of muscular fibres: one, by far the stronger and larger, arising from the inner surface of the inferior posterior margin of the horny plate, and radiating to all parts of the curved ridge, where they are inserted into the ends of the transversely arched plates which sustain the spines; the other set, much less strongly marked, and crossing obliquely over the former, arise from the posterior extremity of the curved ridge of the tongue, and thence pass forward to be inserted successively into the ends of all the transverse plates of the ridge from back to front; the upper fibres are consequently the shortest, the lower the longest.

The former set of fibres, when acting as a whole, will carry downwards and backwards the entire ridge of the tongue. When the muscles of the two sides act alternately, the tongue will be moved from side to side; when the anterior and posterior borders of the muscles act alternately, as it may be supposed they can, the alternate advance and retreat of the spiny ridge will be assisted. The degree of curvature of the tongue and the situation of the curve will materially depend upon the former, as well as upon the latter set of fibres.

On removing the muscles just described from off one side of the tongue, a very beautiful piece of mechanism is brought into view; we find, corresponding to the base of the tongue and the under surface of the buccal mass, two strong semicircular bands of muscle; one, the inferior, Pl. I. fig. 5 *b*, arises from the inferior pointed extremity of the cutting-jaws *e*, directly above the inferior transverse muscle that assists to close the jaws; and thence passes in a curve backwards and upwards, and is inserted into the posterior extremity of the ridge of the tongue. It is to

the under and posterior surface of this band that the muscle (*a*) we have mentioned, as coming down from the upper part of the buccal mass by the side of the œsophagus, is attached. The use of this inferior band is to pull the posterior end of the ridge of the tongue downwards, and thus assist in the rotatory motion of this organ backwards, by which food is carried to the opening of the œsophagus. The other, the superior band, Pl. I. fig. 5 *c*, lies within the curve of the former, and has its ends fixed to the ends of the spiny ridge of the tongue, which it will serve to approximate; but it will more particularly pull downwards and backwards the anterior end of the tongue, being the main agent in its rotatory motion forwards, on account of the muscles which come down from the upper part along the posterior surface of the buccal mass pulling upon the inferior semicircular band to which they are attached, and thus making the posterior end of the tongue a fixed point.

Of the three muscles here last mentioned, the posterior *a*, and the superior *c*, are associated together in action, and are opposed by the inferior *b*, which is also in part intermediate in situation between the others. Altogether they are the chief instruments in producing the rotatory backward and forward motions of the tongue, whilst the muscles that overlie them laterally assist in the rotation, and regulate the place and degree of curvature of the ridge, whilst they can depress the tongue in totality. Now, the nearly circular space that is left between the concave border of the upper semicircular muscle and the concavity of the ridge of the tongue is filled up by a mass of stout, short, transverse fibres *d*, which appear to give strength and stability to the lingual mass, binding strongly together the lateral muscles to which they are fastened, and forming at the same time a firm support to the spiny ridge, and a fulcrum as it were for the semicircular muscles that rotate it.

The inner concave aspect of the horny plates which form the lateral walls of the cavity of the mouth is uncovered for about one-third of its extent at the upper and anterior part, Pl. I. figs. 6 and 8 *a a*, Pl. III. fig. 6 *b*. The rest of the surface is lined by a thick, strong muscular mass, Pl. I. figs. 6 *g* and 8 *e*, and Pl. II. 4. Pl. III. fig. 6 *c*, the fibres of which are inserted into nearly the whole of the lower half of its internal aspect, just above the insertion of the external lateral muscles of the tongue, with which they are blended. From this attachment the fibres pass obliquely upwards, the inner ones being the longest and inclining forwards, and a thick body of muscle is formed, which is terminated above by a flat and broad border, Pl. I. fig. 8 *f* and Pl. II. 4 *b*, Pl. III. 6 *d*, that is free for some distance, lying nearly in contact with the

horny plate: the muscles from the two sides meet together in front of the tongue, and are attached to the inferior pointed extremity of the cutting-jaws, Pl. I. fig. 8 *g*, Pl. II. 4 *c*, Pl. III. 6 *e*, blending there with the muscles that rotate the tongue backwards. On the outer surface of the free part of this cheek-mass, as it may be called, is a thin layer of fibres, Pl. III. fig. 6 *f*, passing at right angles to the bulk of the muscle, and extending from the lower extremity of the cutting-jaws to the side of the œsophagus. At the inferior border of this thin layer lie the salivary glands and duct (*a*).

The use of this mass of muscle appears to be that of accommodating itself to the action of the tongue and assisting it in carrying the food backwards into the œsophagus. May the free edges not be the organs of taste?

The whole of the muscular walls of the buccal cavity are lined, and the wedge of the tongue is covered by a strong membrane continuous with that which lines the œsophagus, and which forms one or two distinct folds, Pl. I. figs. 8 *h* and 6 *h*, over the posterior part of the tongue below the entrance to the œsophagus, but which does not appear to line the horny plates where they are uncovered by muscle, nor to coat the cutting-jaws, and which consequently is not continuous with the membrane which lines the channel of the mouth. It is most probably a mucous membrane.

Lips.—These consist of longitudinal and circular fibres: the longitudinal fibres of the inner lip, Pl. I. fig. 11 *b*, take their origin from a ridge, Pl. II. fig. 5 *a*, on the external surface of the anterior edge of the horny plates, where these become continuous with the cutting-jaws; the fibres arise all the way from the upper to the under margin of the horny plates, inclosing in an elliptical space the cutting-jaws. With these are blended the circular fibres.

The lip thus formed is coated on its inner and part of its outer surface by the lining membrane of the channel of the mouth, so that it projects by a free border, Pl. I. figs. 4 and 6 *b* and 11 *c*, which is wrinkled, into the channel leading to the buccal cavity. This inner lip acts as a sphincter to the orifice of the mouth, and will regulate and assist the approximation of the cutting-jaws; it will also take an active part in the prehension of aliment, which it will carry backwards to the cutting-blades.

The outer lips are prolonged into a tube, Pl. I. fig. 4 *e*, which is the channel of the mouth; they inclose the inner lip. Their longitudinal muscular fibres, Pl. I. fig. 6 *i*, arise from a ridge, Pl. II. fig. 5 *c*, on the sides of the horny plates, immediately behind the origin of the longitudinal fibres of the inner lip, and pass forward to be blended with the integuments at the external

orifice of the mouth. The circular fibres are to be traced from end to end of this tube, but are most abundant at its posterior part, where they form a strong belt or sphincter, Pl. I. figs. 4 *f* and 6 *k*. The use of the outer lips appears to be chiefly confined to sensation, for they are abundantly supplied with nerves, and are retracted by means of their straight fibres when the animal takes its prey.

From the circular belt at the base of the outer lips pass backwards series of fibres, Pl. I. fig. 4 *g g*, the strongest and longest of which are below, corresponding to the foot. These fibres are inserted into the fleshy foot and into the common integument of the sides and top of the body, to which they attach the whole buccal mass, and their office is to retract that mass: this they will do most efficiently when the foot has firm hold of the ground.

From the same belt are seen passing backwards and lying against the external surface of the corneous plates, flat, shining, semitransparent bands of muscle, Pl. I. figs. 4 *h*, 7 *b*, and Pl. II. 3 *a*, which unite and divide irregularly as they are continued to their insertions along the upper and posterior borders of the horny plates. These bands appear to be antagonists to the last-mentioned, and may advance and rotate the buccal mass, during the prehension and cutting of the prey, and probably may assist in retracting the outer lip.

The general characters and the muscular arrangement of the buccal mass do not appear to vary materially throughout the genus *Eolis*. [See that of *E. coronata*, Pl. II. fig. 3.] The lips are nearly the same in all. There are corneous plates and spiny tongue in all. In *E. coronata* however, Pl. II. figs. 6 and 8, the jaws are slightly modified in form. The tongue also varies, and is composed of a single longitudinal row of large, strong, recurved spines or teeth which are minutely pectinated on each side.

In *E. nana* the same compound tooth is found, Pl. II. fig. 10 and Pl. III. fig. 3.

In *E. alba* the tongue is composed of a single longitudinal row of twenty large, simple, recurved spines, Pl. II. figs. 11 and 12, and in *E. olivacea* there are between fifty and sixty transverse rows, each containing about twelve stoutish, almost straight spines, Pl. II. figs. 13 and 14.

The spines of these tongues are very minute, and in *E. papillosa* are not more than one-sixth the thickness of the ordinary hair of the human head. They were often observed to be broken off abruptly, but never bent or partially fractured; hence we were led to suppose that they were not composed of horny tissue, and were induced to try the effect of some reagents upon them. Neither acetic nor nitric acids produced any change in them, but

hydrofluoric acid in the nascent state corroded them extensively, leaving little doubt in our minds that the spines are composed of siliceous matter.

It is difficult to understand how M. de Quatrefages could have mistaken the buccal mass for the stomach, and yet there is no doubt that he has done so in *Eolidina*. From his diagram it appears clear that he has not understood the parts, and his description sets the matter at rest. At page 284 of his memoir, after describing as the œsophagus the channel that leads through the lips to the buccal mass, that gentleman goes on to say, "En arrière de l'œsophage, on aperçoit une masse oblongue, formée par des fibres musculaires entrecroisées. La cavité œsophagienne se continue dans son intérieur en s'y rétrécissant au moins dans l'état de vacuité où était cette portion de l'appareil digestif chez les individus que j'ai examinés. Peut-être est-ce là le lieu où se fait la digestion des substances avalées par l'animal. Du moins, dans un autre mollusque fort voisin de celui-ci, et que j'ai rencontré également à Saint Vast, je trouvai dans un organe entièrement semblable un petit poisson, dont toutes les parties molles avaient entièrement disparu, et dont la colonne vertébrale elle-même commençait à se dissoudre par l'action des forces digestives." And in the next paragraph adds, "Au-delà de ce bulbe stomachale, si l'on peut s'exprimer ainsi, commence le véritable intestin." It appears to us that this naturalist has here drawn a hasty conclusion from an imperfect observation. But afterwards, in a paper on his proposed order *Phlebenterata*, he recognises the tongue of *Actæon elegans*, which also at first sight he mistook for the back-bone of a small fish. Now the tongue of *Actæon* resembles closely that of several small species of *Eolis*, so that we trust that by this time M. de Quatrefages has come to a recognition of the true signification of the parts in *Eolidina paradoxum*.

The account however of the anatomy of this latter animal in the 'Annales des Sciences' for May and June 1843, shows at once that M. de Quatrefages has mistaken the outer lip for the mouth, the channel of the mouth for the œsophagus, the mouth itself for the stomach, and the stomach for the "véritable intestin."

In minute specimens of the *Eolidinæ* the microscope is necessary for the detection of these parts, and the compressor must be adjusted carefully with reference to them: great pressure is requisite to show the tongue. In large specimens the same parts can be dissected out either with or without a lens.

[To be continued.]